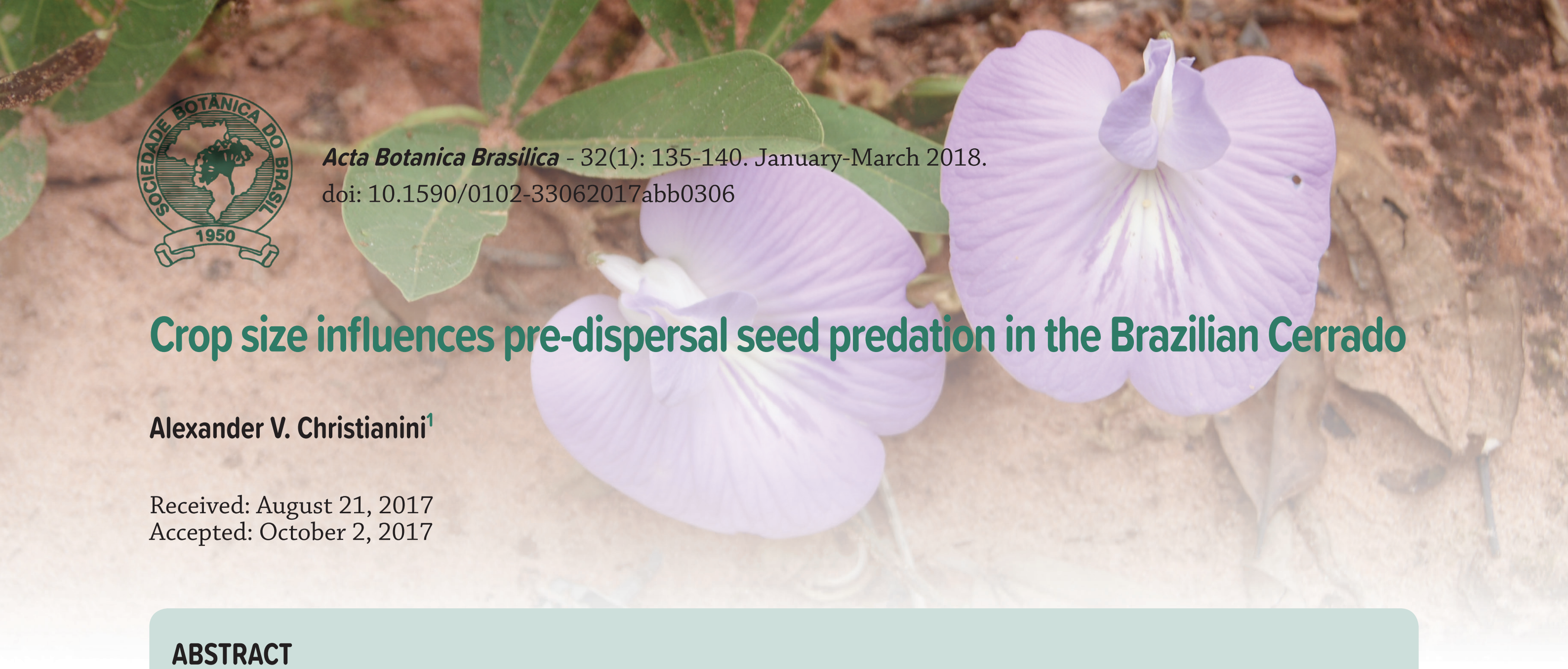

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Crop size influences pre-dispersal seed predation in the Brazilian Cerrado

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ABSTRACT

Many pre-dispersal seed predators are specialized insects that rely on seeds for larval development. These insects may respond to the amount of seeds produced by a plant (i.e. crop size), increasing the proportion of seeds damaged with increases in seed numbers. Large seeds have more resources and spend more time in plants to complete their development and are probably more prone to be preyed on by those insects than small seeds. Here I tested how crop size and seed mass influence pre-dispersal seed predation in plants from the Cerrado savannas of Brazil. I related plant crop size to pre-dispersal seed predation for *Xylopia aromatica* and *Erythroxylum pelleterianum*. A literature review was performed to test if seed mass may explain among-species differences in pre-dispersal seed predation. Pre-dispersal losses increased proportionally to crop size in the two species investigated, but some species show positive or no density-dependent seed predation in literature, indicating that seed losses are not a simple function of crop sizes. Seed mass did not explain pre-dispersal seed loss differences among 14 species with data available. Pre-dispersal losses are often small and probably less important than seed dispersal and establishment limitation for plant recruitment in Cerrado savannas.

Keywords: Brazil, crop size, *Erythroxylum pelleterianum*, savanna, seed number, seed predation, seed size, seed survival, *Xylopia aromatica*

Introduction

Seed crop size is the number of seeds produced by an individual plant in a given fruiting season. Crop size may vary in response to several factors. For instance, plants growing in more fertile soils tend to produce larger crops than those growing in nutrient-poor soils, as well as plants in larger growth forms (e.g. trees compared to shrubs and herbs) (Bogdziewicz *et al*. 2017; and references therein). Individual plant energy reserves, fluctuations in environmental conditions and outcross pollen limitation may produce temporal variations in seed crops (Kon *et al*. 2005). Plants producing smaller seeds also tend to have larger individual seed crops than plants with comparatively larger seeds (Moles & Westoby 2006).

Plants producing more seeds may increase the likelihood of individual seed dispersal and recruitment, because they produce more attractive displays that increase the visits of vertebrate frugivores (Howe & Estabrook 1977). However, some animals attracted to fruiting plants can behave as antagonists, such as granivores. Seeds are often a source of food for many animals, including vertebrates and invertebrates that may prey on the seeds and may thus decrease plant fitness (Hulme & Benkman 2002; Kolb *et al*. 2007). Granivores can eat seeds after or before dispersal acting as post- and pre-dispersal seed predators, respectively. Vertebrates usually have a more prominent

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role as post-dispersal seed predators (but see Francisco *et al*. 2008), while invertebrates are more important in pre-dispersal phase, where seeds are still attached to the plant (Janzen 1971; Hulme & Benkman 2002; Kolb *et al*. 2007). It is common that herbivores feeding on flowers and fruits before dispersal severely decrease seed availability (Kolb *et al*. 2007; Christianini *et al*. 2013), and it is likely that plants producing larger seed crops may also be more attractive to specialized pre-dispersal seed predators (Howe & Estabrook 1977; Kolb *et al*. 2007).

Many invertebrate seed predators (e.g. insects among Coleoptera, Diptera, Hymenoptera and Lepidoptera) rely on seeds as a substrate for their larval development and these interactions can be quite specialized (Janzen 1969; 1971; 1980; Kolb *et al*. 2007). Adult insects oviposit on developing fruits and seeds, and the larvae consume the seed tissue killing the embryo. Seeds are thus critical resources for pre-dispersal seed predator insects. Since larger seeds take longer to complete their development than small seeds, larger seeds offer better and prolonged opportunities to seed predators (Moles & Westoby 2003). As seed predators may severely decrease the availability of seeds for recruitment, they could be a powerful ecological and evolutionary force shaping several plant traits, including crop size of plants (Hulme & Benkman 2002; Kon *et al*. 2005; Kolb *et al*. 2007). Certain plants may produce great amounts of seeds, thus generating a very high but ephemeral concentration of resources in time and space that may satiate seed predators and increase the likelihood of individual seed survival (Kelly & Sork 2002; Kon *et al*. 2005). In this case the amount of seed losses would stop to increase after crop size surpasses a value that saturates the possibility of oviposition and larval growth of insects (predator satiation hypothesis).

In the tropical savannas of Central South America, the Cerrados, regeneration by seed is critical to allow plant colonization of new sites distant from mother plants (e.g. Christianini & Oliveira 2010). However, the low availability of nutrients in soil probably constrains seed production, what decreases seed availability for dispersal and plant regeneration (Salazar *et al*. 2012). Due to low nutrient availability increase in crop size is an unlikely plant strategy to satiate predators and decrease seed losses. However, studies about the impact of crop size on pre-dispersal seed predation are unusual in Cerrado (e.g. Francisco *et al*. 2008) and there is so far no synthesis about pre-dispersal seed predation in this savanna. Here I tested if pre-dispersal seed predation is tied to plant crop sizes in the Brazilian Cerrado using original data from individual plant production in two species and tested if seed mass could be used as a predictor of seed losses based on a synthesis from the literature.

Materials and methods

Original data about the influence of crop size in the amount of pre-dispersal seed predation was obtained from plants growing in the Cerrado from Estação Experimental de Itirapina, a ca. 150 ha state park in Itirapina, Southeast Brazil (22º12'S 47º51'W). The local vegetation is comprised by a Cerrado, the savanna like vegetation that grows on sandy, nutrient-poor soils of Central South America (Oliveira-Filho & Ratter 2002). Annual mean rainfall and temperature is 1,360mm and 21.8ºC respectively, with occasional frost occurring in winter. The local tree and shrub flora is composed by around 100 species with Fabaceae, Myrtaceae and Melastomataceae among the most abundant local plants (Giannotti & Leitão Filho 1992). The park is surrounded by *Pinus* L. and *Eucalyptus* L'Hér. plantations, as well as firebreaks and pasturelands, and is not subjected to fire since ca. 30 years (see Christianini & Oliveira 2013).

Two species of plants common at the study site were used for the tests: the tree *Xylopia aromatica* (Lam.) Mart. (Annonaceae) and the shrub *Erythroxylum pelleterianum* A. St.-Hil. (Erythroxylaceae) (hereafter refereed by genus only). Both species produce diaspores primarily dispersed by birds and reproduce only by seed. *Xylopia* is pollinated by thrips and beetles (Gottsberger 1999), while flowers of *Erythroxylum* are visited by a diverse guild of small insects including bees, wasps and flies (AV Christianini unpubl. res.). *Xylopia* fruits from March to July, and produces dehiscent multiple fruits (divided in follicles) that open to expose ca. 60 seeds in total per fruit (see figure of fruit and a more detailed description in Christianini & Oliveira 2010). *Erythroxylum* fruits from October to December, and produces single-seeded fruits (drupes) with great variation in fruiting among years (AV Christianini unpubl. res.). Both species have their seeds preyed before dispersal by Hymenoptera larvae that develop inside seeds, leaving a small hole after emergence of the adult (Christianini & Oliveira 2010; AV Christianini & PS Oliveira unpubl. res.).

Crop size was estimated on nine individuals of *Xylopia* (seven in 2004 reported in Christianini & Oliveira 2010, plus other two sampled in 2005) and 10 of *Erythroxylum* (in 2004) haphazardly sampled in a 30 ha plot established at the study site. Plants sampled were never closer than 5 m from a reproductive conspecific. Crop sizes were obtained by direct counts on plant crown and also with the aid of seed traps (see detailed methods in Christianini & Oliveira 2010). Briefly, from two to six 0.14 m^2 seed traps were set at ground level beneath individual plant canopies. Seed trap contents were recorded fortnightly, and trap contents were carefully inspected and classified in an exclusive category as unripe (undeveloped fruit or seed), ripe (full seed in a ripe fruit), rotten (seed with signs of decay), or preyed on (with exit holes of pre-dispersal seed predators).

The influence of crop size on pre-dispersal predation was investigated with linear regressions. If pre-dispersal seed predators are not satiated, seed predation should increase isometricaly with crop size. Therefore, to test the influence of crop size on pre-dispersal seed predation first

I fitted data obtained from *Xylopia* and *Erythroxylum* to a power-law function following Harms *et al*. (2000): $\log(y+1) = a + b\log(x+1)$, where x is the crop size per individual plant and y is the number of seeds preyed upon; b is the slope representing the variation in seed predation in relation to crop size and a is the regression intercept. If $b = 1$, seed predation is proportional to crop size (density independent). If $b > 1$, the proportion of seeds preyed on increases with crop size (positive density-dependence). If $b < 1$, the proportion of seeds preyed on decreases with increases in crop size (negative density-dependence; predator satiation). Deviations of the slopes from 1 were tested with the aid of a paired *t*-test comparing the observed number of surviving seeds and the expected if $b = 1$ (Harms *et al*. 2000). Expected values were calculated by substituting b for 1 in regression equations. All tests followed Zar (1999).

To investigate the influence of seed size on the amount of pre-dispersal seed predation at community level I also used linear regressions. First I obtained data from a synthesis of the literature about pre-dispersal seed predation in the Cerrado through a review of published articles. I searched the Web of Science (www.isiknowledge.com) and Scielo (www.scielo.br) platforms using "Cerrado AND seed AND predat* OR graniv*" in topic search in June 01, 2017. The results of the search were screened by title and abstracts. I also looked at the literature cited in the articles obtained by the search to increase literature cover. Articles were excluded if they did not quantify pre-dispersal seed predation or reported only post-dispersal data. If data were presented only in graphs I used ImajeJ (Rasband 1997) to calculate the original data using graph scales. When a species was studied in more than one site or year and data was presented separately, I consider each one as a study case. In these cases I included separate data for each site and year, respectively, otherwise means were used. This procedure allowed a better look at variation within and among species, but may provide pseudoreplication at species level. Therefore, the results should be interpreted with caution. Data on species seed mass were extracted from the original studies or obtained from the literature. This provided pre-dispersal seed predation and mass data for 28 cases involving 14 species distributed in 10 genera (Tab. 1).

Table 1. Summary of studies included in the review about pre-dispersal seed predation in Cerrado. Species are arranged in alphabetic order of family name. *Species that presented data for more than one site or year; †Values refer to range of seed predation for individual plants, mean per study site or years when applicable; # Damaged fruits; ‡ Estimate of seed loss may be slightly inflated due to post-dispersal seed predators; na = not available or evaluated in the study.

Family	Species	Seed mass (g)	Main pre-dispersal seed predator	Pre-dispersal seed loss (%)†	Relation of pre-dispersal loss with crop size (slope)	Reference
Annonaceae	*Annona crassiflora*	0.66	Hymenoptera (Eurytomidae)	53.8%‡	na	Golin *et al*. 2011
	Xylopia aromatica	0.06	Hymenoptera (Pteromalidae, Eurytomidae)	0.8%-10%	Isometric with crop size (1.132)	This study
Caryocaraceae	*Caryocar brasiliensis*	1.1	Birds	18%-43%	Positive density dependence (na)	Ragusa-Neto 2011
Erythroxylaceae	*Erythroxylum pelleterianum*	0.041	Hymenoptera	0%-0.7%	Isometric with crop size (0.6915)	This study
Fabaceae	*Copaifera langsdorffii**	0.476	Coleoptera (Curculionidae)	8.2%-15.9%	No effect in one study (na)	Fagundes *et al*. 2013; Souza & Fagundes 2017
Malvaceae	*Eriotheca gracilipes*	0.3	Birds	0%-100%	Positive density dependence (1.21)	Francisco *et al*. 2008
Mimosaceae	*Mimosa clausseni**	0.113	Coleoptera (Curculionidae, Bruchidae) and birds	19.8%-56.5%	na	Simon & Hay 2003
	M. decorticans	0.388	Coleoptera (Curculionidae, Bruchidae)	6.1	na	Simon & Hay 2003
	M. heringeri	0.347	Coleoptera (Curculionidae, Bruchidae)	9.2	na	Simon & Hay 2003
	M. setosissima	0.317	Coleoptera (Curculionidae, Bruchidae)	2.3	na	Simon & Hay 2003
Solanaceae	*Solanum lycocarpum*	0.038	Rodents	14%-75%#	Positive density dependence (1.26)	Briani & Guimarães Jr. 2007
Vochysiaceae	*Callisthene fasciculate**	0.082	No seed predator found	0%	na	Custódio *et al*. 2014
	*Callisthene major**	0.588	Coleoptera (Curculionidae)	0%-51.34%	na	Custódio *et al*. 2014
	*Qualea multiflora**	0.0746	Coleoptera (Buprestidae) and maybe Hymenoptera	0%-43.97%	na	Custódio *et al*. 2014
	*Qualea parviflora**	0.033	Coleoptera (Buprestidae) and maybe Hymenoptera	20%-60.23%	na	Custódio *et al*. 2014

Results

There was great variation in the crop sizes of individual plants. For *Xylopia*, crop sizes varied between 39 and 627, a 1,500 % difference (see also Christianini & Oliveira 2010), while for *Erythroxylum* crop sizes varied between 252 and 4828, a 1,800 % difference (AV Christianini & PS Oliveira unpubl. res.). Damage from pre-dispersal seed predators was relatively low, from 0 % to 13.7 % of the seeds of *Xylopia* and *Erythroxylum* (Fig. 1). Pre-dispersal seed predation followed crop size variation in *Xylopia* (r^2= 0.56 for a log-log linear regression: Pre-dispersal predation = -1.646 + 1.132 (Crop size); $F_{1,7}$=9.08; p=0.019), and the slope of the regression did not differ from 1 (paired *t*-test: *t*=0.0005; df=8; p=0.99) (Fig. 1). A qualitative similar result was obtained with the inclusion of data only for 2004 (seven trees) in the analysis (results not shown). The relation between crop size and pre-dispersal seed predation in *Erythroxylum* followed the same trend (r^2=0.54: Pre-dispersal predation = – 1.7148+ 0.6915 (Crop size); $F_{1,8}$=9.66; p=0.014), and the regression slope also did not differ from 1 (*t*=0.002; df = 9; p = 0.998) (Fig. 1). Thus, for both species there was an isometric increase in seed predation with increase in crop size.

The literature review indicated great among-species variation in the amount of seed predation, from 0 % in *Callisthene fasciculate* (Custódio *et al*. 2014) up to 100 % in *Eriotheca grassilipes* (Francisco *et al*. 2008) (Tab. 1). There was also substantial within-species variation among years (*e.g*. 8.2 % and 15.9 % of seed predation in two years for *Copaifera langsdorffii*) (Souza & Fagundes 2017) and sites (0 % and 51.3 % seed predation in two different sites for *Callisthene major*) (Custódio *et al*. 2014) (Tab. 1). Pre-dispersal seed predation was performed by birds or rodents in four species (27 %) while insects (Coleoptera and Hymenoptera) preyed on seeds of 10 (67 %) plants. One species (*Callisthene fasciculate*) had no seed predation recorded (Tab. 1). These large variations in pre-dispersal seed predation were not influenced by seed size ($F_{1,26}$=0.239; r^2=0.01; p=0.634) (Fig. 2).

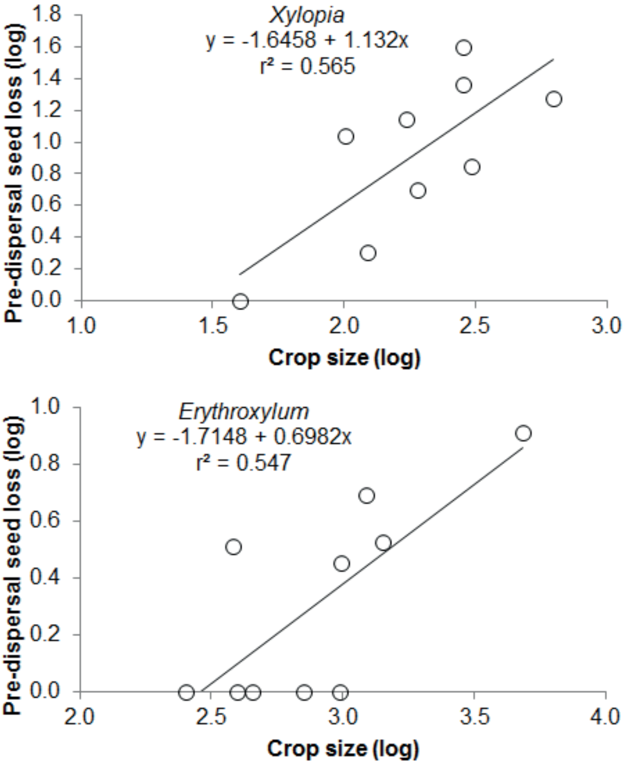

Figure 1. Relationships between individual plant crop sizes and the amount of pre-dispersal seed predation observed for plants of *Xylopia aromatica* (above) and *Erythroyxlum pelleterianum* (below) in a Cerrado from southeastern Brazil. Seed predation was influenced by crop size variation for both species but regression slopes did not differ from 1.

Discussion

There is a diversity of responses of pre-dispersal seed predators to crop size variation in Cerrado. While pre-dispersal losses are proportional to crop size in *Xylopia* and *Erythroxylum*, for three other species (*Caryocar brasiliensis*, *Eriotheca gracilipes* and *Solanum lycocarpum*) the proportion of pre-dispersal losses increases with crop sizes indicating that seed predators are positively influenced by seed density (Tab. 1). For another species (*Copaifera langsdorffii*) increments in crop sizes between years were not followed by changes in seed losses, suggesting predator satiation (Souza & Fagundes 2017). Enhancement of seeds losses with increasing seed density may constrain the evolution of large crop sizes. Indeed, *Xylopia* and *Erythroxylum* produce much larger annual crops than those plants affected by positive

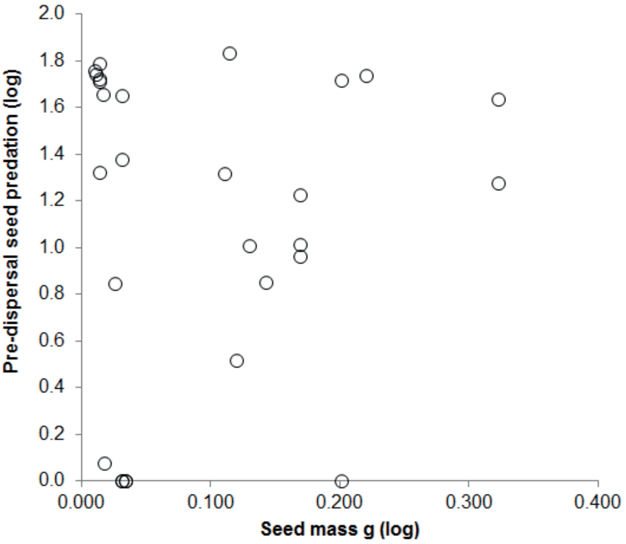

Figure 2. No effect of seed mass variation on the amount of pre-dispersal seed predation recorded in studies with plants from the Cerrado. Data was obtained from 28 study cases with 14 species found in a literature search (see details in Materials and methods).

density-dependence seed predation, although other traits such as growth form and seed mass may also be under these differences (see Moles & Westoby 2006). Variable relationships between crop size and the likelihood of pre-dispersal seed predation are also reported in other systems (Augspurger 1981; Jordano 1987; Brody & Mitchell 1997; Kelly & Sork 2002; Bogdziewicz *et al*. 2017), including great among and within species variation in pre-dispersal seed predation for other tropical savannas (Ernst *et al*. 1990; Custódio *et al*. 2014).

What are the consequences of the amount of seed losses for the plants? Unless the regeneration of plants are seed limited (Ferreira *et al*. 2011; Salazar *et al*. 2012), pre-dispersal seed predators are unlikely to decrease substantially plant fitness by reducing the amount of seeds available for recruitment. There is evidence that seed and dispersal limitation decrease the opportunities of recruitment of *Xylopia* and *Erythroxylum* to some extent (Christianini & Oliveira 2010; 2013). However, the small amount of seeds lost to pre-dispersal predators does not seem to be enough to control the recruitment of these plants at the study site, with dispersal and establishment limitation playing a more important role (Christianini & Oliveira 2010; 2013) as well as for other species in Cerrado (Ferreira *et al*. 2011; Salazar *et al*. 2012).

Data about the population abundance and fluctuation of the pre-dispersal seed predators are scarce, but the relative isolation and small size of the Cerrado fragment studied might be influencing the results. Pre-dispersal seed predation is often performed by specialized herbivores (Janzen 1969; 1971; 1980; Kolb *et al*. 2007). These herbivores often decrease in abundance and diversity following habitat fragmentation and declines in their host plants (Ruiz-Guerra *et al*. 2010). However, *Xylopia* and *Erythroxylum* populations are among the most abundant plants at the study site (V Mariano & AV Christianini unpubl. res.), and there is evidence that crop size of *Erythroxylum* is not influenced by edge effects (Christanini & Oliveira 2013). Therefore, seed availability is probably not constraining the populations of the insect seed predators recorded. On the other hand, the high abundance of these plant species could indicate that predator satiation could be taking place at larger spatial scales beyond individual plants. Seed predators may respond to the density of seeds of several individual plants at close distance from each other, and to the costs and benefits of searching and moving among different plants or patches (Kelly & Sork 2002; Ragusa-Netto 2011). Thus the satiation of seed predators could occur at patch rather than individual plant level (García & Chacoff 2007). Unfortunately there is no data available to evaluate this hypothesis at the moment. Seed predation may also be subjected to temporal fluctuations that influence the satiation of predators (Kelly & Sork 2002; Kon *et al*. 2005; Żywiec *et al*. 2013; Bogdziewicz *et al*. 2017). For instance, in tropical dry forests of Mexico, *Erythroxylym havanense* shows density-dependent seed predation in some years, while in other years seed predation fluctuate at random (Boege & Domínguez 2008). There is also the possibility that plants aborted reproductive structures and the infested seeds before maturation due to herbivore attack (Christianini *et al*. 2013; Custódio *et al*. 2014), what may produce underestimates of seed losses measured latter during fruit maturation. Although I cannot eliminate this possibility, a visual inspection of aborted seeds sampled in traps showed no evidence of damage by seed predators, suggesting that *Xylopia* and *Erythroxylum* do not selectively aborted infested fruits (see also Boege & Domínguez 2008 for *Erythroxylum havanense*).

Seed mass and investment in protective tissues are often correlated (Moles & Westoby 2003; Ramírez & Traveset 2010). Indeed, increases in seed mass and fiber, and a decrease in starch content decrease seed losses to pre-dispersal seed predators in savannas from Central Venezuela (Ramírez & Traveset 2010). However, contrary to the expectation seed mass has no influence in pre-dispersal seed predation at community level in Cerrado. This result agrees with data compiled for several localities in Australia and around the world (Moles *et al*. 2003). If protective tissues alone drive pre-dispersal seed losses, larger seeds would suffer less predation in cerrado which is not the case. Specificity of seed predators, seed abundance, chemical traits and plant phenological patterns may also drive the interactions between a given seed predator and a plant (Janzen 1969; 1980; Kolb *et al*. 2007; Ramírez & Traveset 2010). All those traits may influence the levels of seed predation detected, but currently there are no data available for Cerrado plant communities to evaluate their influences in detail. However, data from the current review suggest that pre-dispersal seed losses are correlated with crop sizes for most species that investigated this topic (five in six cases, Tab. 1), irrespective of seed size. For instance the crop size variation of the largest-seeded plant (*Caryocar brasiliensis*) and some of the smallest ones (*Erythroxylum pelleterianum*) in the sample produce similar responses of seed predators. Therefore, plant crop size seems to be a better predictor of seed losses than seed mass and it is possible that among year fluctuations in crop sizes may benefit plants from Cerrado. Populations of specialized seed predators may decline in years with no or low seed production, being more easily satiated in a subsequent year of high seed production as predicted by the predator satiation hypothesis in mast seeding species (Kelly & Sork 2002; Kon *et al*. 2005). Future studies may evaluate this possibility.

In summary, individual plant crop size has variable but often a positive correlation with the amount of pre-dispersal seed losses in the Cerrado, while among species seed mass differences is a poor predictor of pre-dispersal seed predation. Since crop size may be under negative selection by predators and positive selection by pollinators and seed dispersers (Howe & Estabrook 1977; Kon *et al*. 2005; Boege & Domínguez 2008; Bogdziewicz *et al*. 2017) it would be interesting to evaluate the net effect of crop size variation in plant recruitment in this savanna. At the same time, increase the knowledge about the biology of seed predators may allow us to test more refined hypothesis about the drivers of pre-dispersal seed predation and how to conserve the tremendous diversity of interactions in this species rich savanna.

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